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NOTES ON MOUNTAIN MIDGES (DEUTEROPHLEBIIDAE) WITH A DESCRIPTION OF THE IMMATURE STAGES OF A NEW SPECIES FROM COLORADO[1]

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While studying the bottom fauna of two northern Colorado mountain streams during August, 1944, several graduate students in one of the writer's classes collected larval and pupal stages of one of the least-known and most unusual families of Diptera, the Deuterophlebiidae, or mountain midges. Subsequent searching by the writer has shown that these bizarre aquatic forms are widely distributed, though not abundant, in northern Colorado.

An examination of the literature reveals that the only North American record of this family is a sketchy description and photograph (Muttkowski, 1927) based on a single larva from the Yellowstone River, Wyoming. However, several species, all belonging to the genus *Deuterophlebia*, have been more completely described from Japan and from a wide area on the Asiatic mainland. Although the Colorado specimens belong to the same genus, they undoubtedly represent a new species.

Deuterophlebia coloradensis, new species

LARVA

GENERAL LARVAL CHARACTERISTICS: The larvae are quite similar to those of other species. The general body shape is plano-convex. The head is free, distinct, flat, and wide, with long branched antennae. The thoracic segments are all distinct and separated by lateral incisions. The abdomen consists of eight distinct segments, the fourth being slightly the widest. Each of the first seven segments bears a pair of large, stout, lateral prolegs supplied with numerous rings of minute claws at the ends. The last abdominal segment is provided with two tapered, terminal processes and five shorter, soft, rounded lobes. There are no stigmata. The dorsal surface of the entire body, including prolegs, is covered with a very fine dense pubescence. Coloration ranges from light to dark brownish, although the head is almost blackish because of greater sclerotization. Twelve well-extended mature larvae were collected, the length range being 3 to 4.5 mm., and the average being 3.9 mm.

HEAD: The head is rather flat and slightly wider than long. The unique branched antennae are long and originate on large tubercles. The proximal segment is stout, roughly cyclindrical, and about four times as long as wide. The short ventral branch is cylindrical, blunt, and about as long as the proximal segment. The dorsal branch gradually tapers to a point and is just twice as long as the ventral. Both branches are only slightly sclerotized and are supplied with an abundance of minute tactile spots (Brodsky, 1930). The eyespots are small black areas posterior to the bases of the antennae. There are usually nine tufts of small setae on the head capsule near the base of each antenna.

The labrum is a thick structure which projects anteriorly. On its ventral surface it bears two densely setaceous ridges which are widely separated distally and converging near the base of the labrum. The epipharynx is a median lobe situated just posterior to the point of convergence of the setaceous ridges. Pulikovsky (1924) has probably misidentified the epipharynx from serial sections, calling it the hypopharynx.

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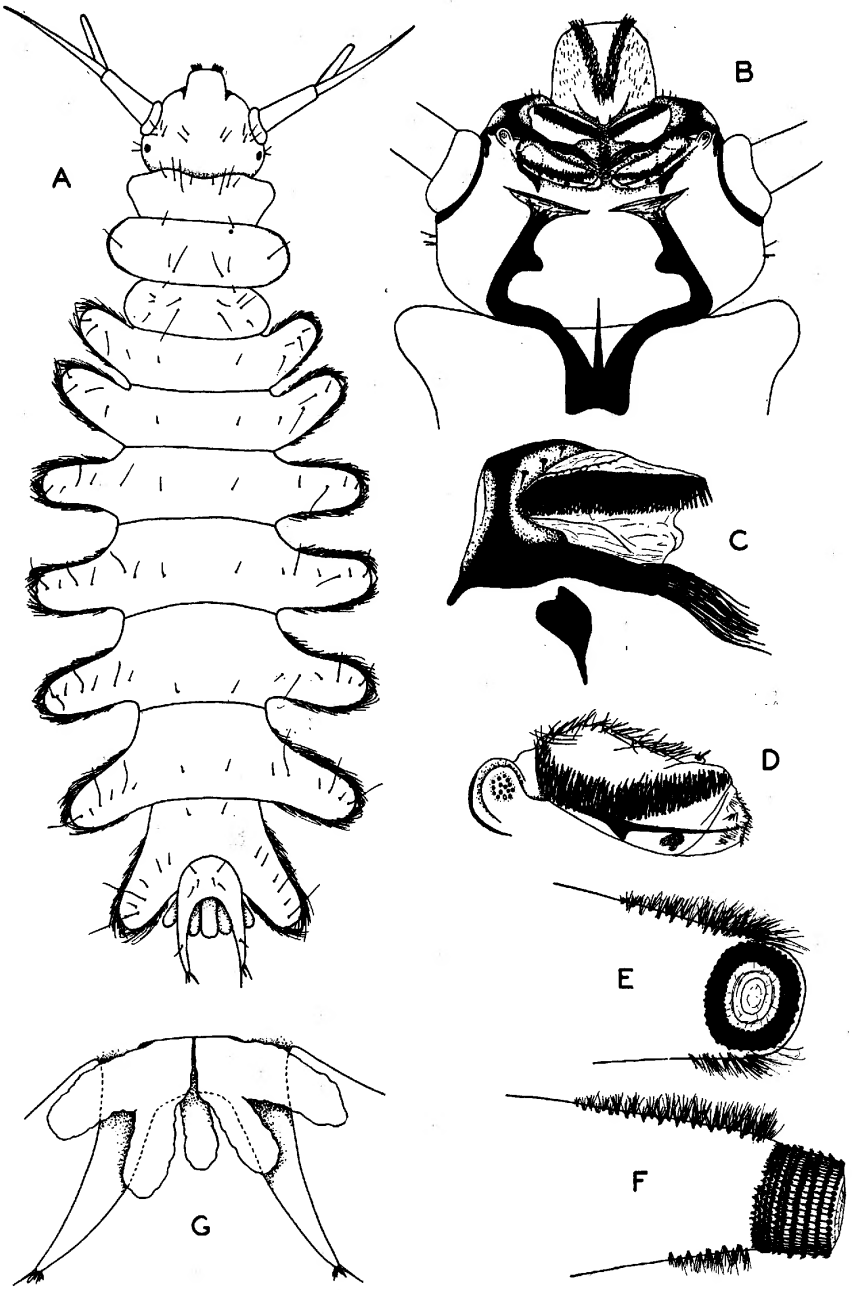

Fig. 1. Anatomical details of the mature larva of *Deuterophlebia coloradensis*, new species. A, dorsal view (fine pubescence omitted), × 28; B, ventral view of head; C, ventral view of right mandible; D, ventral view of right maxilla; E, ventral view of proleg in normal position, curved toward observer; F, ventral view of proleg which has been straightened out to show relationships of rings of hooks; G, ventral view of posterior end.

The mandibles are of a peculiar construction (fig. 1C). The basal portion consists of a rigid, heavily sclerotized ring which is very narrow ventrally and broad dorsally. At the median posterior margin of this ring is a tuft of long bristles directed toward the mouth opening. There are three short setae on the anterior part of the ring. The remainder of the mandible consists of a soft portion capable of being extended or folded back into the sclerotized ring. Near the anterior margin it bears two comb-like rows of heavy teeth, one superimposed upon the other. The teeth of the ventral comb point backward, but those of the dorsal comb point obliquely outward. A flat, heavily sclerotized piece is attached to the cuticle at the base of the mandible; Pulikovsky believes that it serves for the attachment of muscles.

The maxillae are highly developed but simple in form (fig. 1D). The maxillary lobe is a large, soft, transverse structure supported by a thin sclerotized rod. On the face of the lobe there is a dense comb-like device consisting of several irregular rows of heavy teeth, and along the front margin there is an irregular row of setae. At the median margin there are several short rows of fine setae, and near the posterior margin is a small irregular area which appears to consist of many minute granules. The palp is lateral to the maxillary lobe and is situated on a strongly sclerotized prominence. It is small, flat, and rounded and bears a cluster of chitinous buds.

The labium is absent, but, as pointed out by Pulikovsky, the maxillae oppose each other in such a fashion as to close effectively the buccal cavity and function as a labium.

The mandibular combs are said to be used for scraping diatoms and other algae from rock surfaces, while the mandibular bristles and maxillary combs strain this food from the water and guide it into the mouth.

THORAX: The thoracic segments are flat and distinctly separated from each other. The mesothorax is the widest and longest of the three, and the metathorax is narrowest and shortest. The prothorax slightly overlaps the posterior margin of the head. The prothorax, mesothorax, and metathorax have about eight, eight, and 12 setae, respectively, on the dorsal surface.

ABDOMEN: The abdomen consists of eight segments, increasing in size in the middle so that the fourth segment is slightly larger than either the third or fifth. Each of the first seven segments bears a pair of large prolegs. These prolegs originate laterally on the segments, but are curved downward distally so that the flattened pad-like tips come in contact with the substrate. The third, fourth, and fifth pairs of prolegs extend at almost right angles from the long axis of the body, but the first and second extend obliquely forward, and the sixth and seventh obliquely backward. At the end of each proleg, and surrounding the flat-

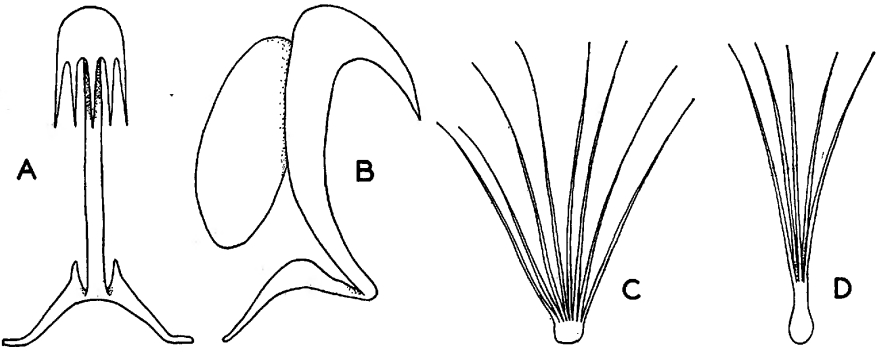

Fig. 2. Cuticular structures of the larva of *Deuterophlebia coloradensis*, new species. A, fronta view of claw of proleg; B, lateral view of claw of proleg; C and D, typical branched hairs from proleg.

tened tip, is a series of rings of peculiar, minute, sclerotized claws (figs. 1E, F, 2A, B). Each claw is roughly Z-shaped and consists of a curved, ctenoid portion with five teeth and a long, flat, keeled stalk or pedicel, the basal portion of which is bifurcated (fig. 2A, B). The claws of the more distal rings are the longest. The number of rings of claws on the first proleg is nine for all 12 larvae examined, but the number varies inconsistently from eight to 12 on the other prolegs, although there are usually nine to 11. Much of this variation is probably due to the fact that many of the claws or incomplete rings of claws are lost or torn off during the normal activities of the larvae. Also, the rings of claws are sometimes obviously incompletely formed and may extend only a third of the way around the proleg. On a proleg of one paratype, for example, there are eight rings of claws on the outer surface and 11 on the inner. Along the anterior and posterior margins of each proleg there are three to five rows of branched, brush-like hairs (fig. 2C, D). The length of the hairs increases gradually from the basal to the distal portion of the prolegs.

The prolegs are specialized for clinging to the rocks of stream beds in swift currents, the chitinous pad at the tip of each proleg together with the surrounding rings of claws acting like a somewhat imperfect sucking disc. The action and detailed anatomy of this apparatus have been explained by Pulikovsky. Unlike blepharocerid larvae, *Deuterophlebia* does not cling tightly to the substrate and can be easily removed with forceps or fingers.

The last abdominal segment (fig. 1G) is comparatively small and is provided with two long, tapering, sclerotized processes, each of which bears three or four flat terminal setae. On the ventral side of this segment and partially hidden by it are five blunt, cylindrical, delicate lobes or sacs arranged around the anal opening. One lobe is median and slightly dorsal, and the other four are paired, lateral, and more ventral. They have a very thin cuticle, large hypodermal cells, and are devoid of tracheation. As emphasized by Pulikovsky, it is likely that these lobes may function as blood gills. The fact that the tips of the Malpighian tubules project out into four of these lobes, however, may indicate that they have some osmoregulatory or excretory function.

In addition to the fine, dense pubescence on the dorsal surface, each abdominal segment and its two prolegs bear a total of about 12 setae. The ventral surface of the abdomen is naked.

LARVAL DEVELOPMENT: Both Kitakami (1938) and Brodsky (1930) have shown quite conclusively that Japanese and continental Asiatic species of *Deuterophlebia* have four larval instars. These stages may be distinguished on the basis of three different morphological features: the length ratio of the segments of the antennae, the number of rings of claws on the prolegs, and the total body length. All 12 specimens of *Deuterophlebia coloradensis*, however, seem to belong to a single, last instar. There are no significant differences in the number of rings of claws, the ratio of the length of the antennal segments is the same, and all larvae are in the same general size group. Four paratype specimens were approaching pupation when collected, and the developing pupal respiratory filaments can be easily seen through the integument in the lateral portions of the prothorax. The three smallest specimens, ranging from 3 to 3.3 mm. in length, have a more transparent integument than the others, but it is likely that they had passed through an ecdysis only a short time before being collected. Kitakami has shown that such larvae are usually relatively small.

TYPE MATERIAL: Holotype mature larva from Boulder Creek, Boulder County, Colorado, July 31, 1944, elevation 1810 meters; in the American Museum of Natural History. Paratypes are in the author's collection.

PUPA

GENERAL CHARACTERISTICS: Six complete pupae and six empty pupal cases were collected. Superficially the pupae resemble blepharocerids and are adapted to a life on rocks in swift streams. They are broadly oval, only slightly convex

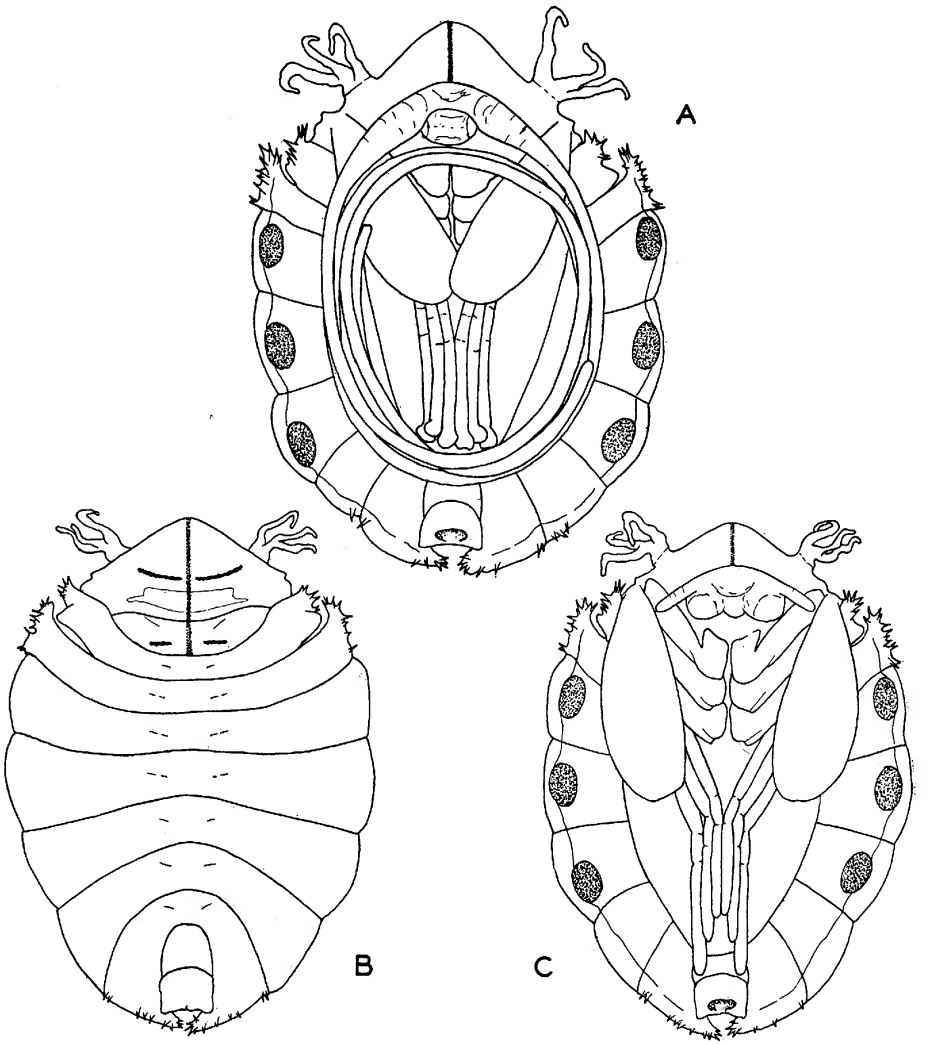

Fig. 3. Anatomical features of the pupae of *Deuterophlebia coloradensis*, new species. × 29. A, ventral view of male pupa; B, dorsal view of female pupa; C, ventral view of female pupa.

dorsally, and flat ventrally. The dorsal surface is strongly sclerotized and dark brown or blackish in color, chiefly due to an abundance of dark, round to oval granulations on the cuticle. These granulations range from 3.5 to 6.5 microns in diameter. The ventral surface is covered with a thin, colorless cuticle, especially in the younger pupae.

Sexual dimorphism is obvious. The female has short antennal sheaths which scarcely reach to the base of the wing sheaths, but the male has enormously long antennal sheaths, each of which is coiled in about two and three-quarters large, elliptical rings on the ventral surface (fig. 3A). One pupa and one pupal case are males; the other 10 specimens are females.

There is a wide range in total body length, the extremes being 2.1 and 2.9 mm., and the average being 2.3 mm. Brodsky and Kitakami have noted comparable variations in other species.

HEAD: The head lies on the ventral side of the body and is completely hidden by the thorax. The head of the male is much larger than that of the female.

THORAX: The prothorax is entirely fused with the mesothorax, and the latter is roughly triangular in shape with a very broad base. On the anterior lateral margins of the mesothorax are two respiratory processes. Each consists of a short broad base and three slender, elongate, irregularly bent filaments. Somewhat similar structures occur in some Chironomidae and Simuliidae. The metathorax does not reach the lateral margins of the body but is completely enclosed between the mesothorax and first abdominal segment. Extending throughout the length of the thorax is a longitudinal seam consisting of closely arranged granules. At the end of the pupal stage this seam splits open and permits the emergence of the imago. In the middle of the mesothorax is a pair of thin, transverse, heavily sclerotized bands, one on each side of the midline. Two similar but shorter bands occur on the metathorax.

Ventrally the sheaths containing the thoracic appendages may be seen. The oval-oblong wing sheaths extend as far as the fourth abdominal segment. The femoral portions of the leg sheaths extend anteriorly and laterally, but the succeeding portions are directed posteriorly near the midline. The tips of the leg sheaths in the male are swollen, due to the large empodia of the imago.

ABDOMEN: The first and second abdominal segments are very narrow and project anteriorly at the lateral margins in the form of prominences bearing small, stout, thorn-like spines. The number of thorns is highly variable and has no relation to the size or sex of the pupa. In the 12 specimens available the number on each side of the first abdominal segment ranges from four to 10 with an average of seven, and on the second segment the number ranges from eight to 16 with an average of 11. The seventh segment projects inward on each side at its posterior margin and almost completely encloses the succeeding segments. Along the lateral margin of the abdomen near the suture between the sixth and seventh segments is a group of none to nine thorns with an average of four. Along the posterior margin of the seventh segment is a group of similar thorns ranging from three to 10 on each side with an average of seven. The eighth segment is small and enclosed by the seventh and ninth. The ninth segment is completely fused with the tenth and is roughly square in shape.

Near the lateral margins of the ventral surface of the third, fourth, and fifth abdominal segments are paired, oval, adhesive pads by which the pupa remains tightly attached to the substrate. These pads do not project from the general body surface and appear to be composed of small black granules and irregular patches. Presumably some adhesive substance is produced in these six areas. The extreme lateral portions of the abdominal segments are slightly more flattened than the rest of the body.

TYPE MATERIAL: Holotype female pupa from Boulder Creek, Boulder County, Colorado, July 31, 1944, elevation 1810 meters; in the American Museum of Natural History. Paratypes are in the author's collection.

ADULT

Thus far no adult specimens have been collected. Actually very few emerged Deuterophlebiidae imagoes have ever been found. Edwards (1922) collected two male *D. mirabilis*, Kitakami (1938) collected 57 female *D. nipponica* over a period of 12 years, and Yie (1933) found one female of the same species. All other records and descriptions of imagoes are from specimens which have been dissected from mature pupae. It is unfortunate that none of the pupae of *D. coloradensis* contain adults which can be removed and studied in detail. Kitakami believes that active imagoes are difficult to collect because they emerge during the night or very early morning and live for only a few hours.

The unusual nature of the imago has been emphasized by other writers. Among some of the more striking features are: the complete absence of mouthparts, the immense wings with elaborate secondary and concentric transverse folds, and the extremely long antennae in the male.

HABITAT AND DISTRIBUTION

Scattered larvae and pupae were collected from several northern Colorado mountain streams wherever diligent searching was carried out. These streams and the altitudes of collecting localities are as follows: Thompson River, 2750 meters; St. Vrain Creek, 1690 meters; North Boulder Creek, 2750 and 2190 meters; Boulder Creek, four localities between 1680 and 2100 meters. The early belief that *Deuterophlebia* is restricted to mountain streams at very high altitudes has now been largely discarded. Brodsky (1930) found *D. mirabilis* as low as 1000 meters in central Asia, and Kitakami (1938) reported *D. nipponica* from Japanese streams at altitudes of 150 to 1600 meters. Certainly the genus is not confined to cold waters, since some Colorado specimens were taken from streams having temperatures as high as 18.5° C. Other workers have collected larvae and pupae from waters having temperatures ranging from 4 to 18° C.

Deuterophlebia coloradensis is not restricted to torrents. Although some specimens were found on rocks near the base of a waterfall, others were collected from streams with a relatively smooth rubble bottom where the current was not over 2 meters per second. All specimens were on the upper surface of rocks and pebbles where they were exposed to the full force of the current.

No attempt was made to collect *D. coloradensis* before August 1; consequently no spring and early summer data are available concerning its abundance and occurrence. Nearly all of the larvae and pupae were collected in August, 1944, a few being found early in September. Intensive searching between September 15 and October 2 failed to reveal a single specimen. Kitakami collected *D. nipponica* larvae and pupae from March through November, but Brodsky collected immature stages of *D. mirabilis* between June and October in the more rigorous climate of the mountains of central Asia. The latter's contention that wintering-over occurs in the early larval instars seems to be a logical one, and presumably it applies to *D. coloradensis*. Yie (1933), on the other hand, believes that the larval period is very short in *D. nipponica* and is probably completed in two weeks. Both he and Kitakami contend that there are several generations per year.

The relative rarity of males has resulted in considerable speculation, and Kitakami has even suggested parthenogenetic development by the great majority of individuals.

COMPARATIVE NOTES ON THE SPECIES OF *DEUTEROPHLEBIA*

As shown in table 1, the genus *Deuterophlebia* consists of only four well-established species, the imagoes being known for only two of these. The paper of Pulikovsky (1924) requires some discussion with reference to this table. It appears that her specimens from Altai mountain streams consisted of at least two species, although she thought that she was dealing with a single species, which she designated as *Deuterophlebia* sp. Two distinct types of pupae are described in her paper, one with a long spine at the base of the thoracic respiratory filaments on each side of the mesothorax, and one without. The latter specimens were also examined by Brodsky (1930), and he appears convinced that they are identical with his own specimens of *D. mirabilis* Edwards. The specimens with the two thoracic spines, however, are unique and undoubtedly constitute a distinct species. This contention is shared with Brodsky and Kitakami. It is indicated as *Deuterophlebia* sp. in table 1. Pulikovsky dissected some female imagoes from the spined pupae, but her description of them is so general that it cannot be used for a comparison with imagoes of other species. The larvae described by Pulikovsky were also studied by Brodsky, and he is satisfied that they are *D. mirabilis*. Since larvae of different species are often

TABLE 1

SUMMARY OF THE GEOGRAPHICAL DISTRIBUTION, DESCRIPTIVE LITERATURE, AND PUBLISHED RECORDS OF THE SPECIES OF *Deuterophlebia*

Species	Known geographical distribution	Stage	Described and (or) recorded by
D. mirabilis Edwards	Mountainous areas of central Asia; roughly between 34° and 46° north latitude, and 69° and 99° east longitude	Larva	Pulikovsky (1924, as *Deuterophlebia* sp.); Brodsky and Brodsky (1926, as *Deuterophlebia* sp.); Brodsky (1930)
		Pupa	Pulikovsky (1924, as *Deuterophlebia* sp.); Brodsky and Brodsky (1926, as *Deuterophlebia* sp.); Brodsky (1930)
		Adult male	Edwards (1922); Brodsky (1930)
		Adult female	Brodsky (1930)
D. nipponica Kitakami	Widely distributed on the Japanese islands of Honshu and Kyushu	Larva	Kitakami (1929, as *Deuterophlebia* sp.); Kawamura (1932, as *Deuterophlebia* sp.); Yie (1933, as *Deuterophlebia* sp.); Kitakami (1938)
		Pupa	Kitakami (1929, as *Deuterophlebia* sp.); Kawamura (1932, as *Deuterophlebia* sp.); Yie (1933, as *Deuterophlebia* sp.); Kitakami (1938)
		Adult male	Kitakami (1938)
		Adult female	Kitakami (1929, as *Deuterophlebia* sp.); Kitakami (1938)
D. tyosenensis Kitakami	Northern Korea	Larva	Kitakami (1938)
		Pupa	Kitakami (1938)
D. coloradensis, new species	Northern Colorado	Larva	Pennak (present paper)
		Pupa	Pennak (present paper)
Deuterophlebia sp.	Yellowstone River and Lost Creek, Yellowstone National Park, Wyoming	Larva	Muttkowski (1927)
		Pupa (?)	Muttkowski (1927)
Deuterophlebia sp.	Convict Creek, Mono Co., Calif.	Larva	Pennak (present paper)
Deuterophlebia sp.	Rock Creek, Benton Co., Oregon	Larva	Pennak (present paper)
Deuterophlebia sp.	Altai Mountains	Larva (?)	Pulikovsky (1924)
		Pupa	Pulikovsky (1924)
		Adult female	Pulikovsky (1924)

similar in their more prominent characteristics, it is possible that some of the specimens were of the other species.

Muttkowski (1927) found a single larval specimen in the Yellowstone River, Wyoming. Since it was less than 1 mm. long, it was probably in the first instar. His description is very general, but it is not unlikely that it is *D. coloradensis*. Muttkowski also collected eight or nine specimens in the Yellowstone River and Lost Creek, Wyoming, which he thought *may* have been deuterophlebiid pupae; no description is given in his paper, however. Because of these uncertainties, Muttkowski's material is indicated in table 1 as *Deuterophlebia* sp.

During the organization of the present paper the author wrote to many institutions in the United States where large Diptera

collections are kept, in an attempt to obtain additional, unpublished data. This correspondence netted only two new records. One was received from Dr. O. A. Johannsen, Cornell University, who stated that H. J. Reynor and R. S. Nielson collected some larvae in Convict Creek, Mono Country, California, in August, 1937, at an elevation of 7000 feet. The specimens "resembled Muttkowski's species." Their whereabouts is unknown.

The other new record involves a single larval specimen. It was collected in Rock Creek, Philomath, Oregon, in May, 1942, and through the kindness of Dr. H. A. Scullen of Oregon State College the writer was permitted to examine it. In its morphological features it is indistinguishable from mature *D. coloradensis* larvae. A more reliable identification, however, must be delayed until the pupa can be examined. In the meantime the larva is recorded as *Deuterophlebia* sp. in table 1.

In general, the mature larval stages of the four well-established species of *Deuterophlebia* are very similar and often cannot be distinguished from one another on the basis of gross structure. This is evident from table 2 where three important morphological features are compared. It is unfortunate that other papers do not contain accurate descriptions of anatomical details, especially mouthparts and setation, which might be useful and definitive criteria for separating species.

The pupal stage, on the other hand, is much more distinctive, and identifications may be easily made by means of certain features of the thoracic region, as indicated in the following key.

KEY TO THE PUPAE OF *Deuterophlebia*

1. With one or two long, narrow spines on the thorax near each group of respiratory filaments.....2
   Without such spines.....3
2. With two long thoracic spines on each side; northern Korea.....
   .....*D. tyosenensis* Kitakami
   With one long thoracic spine on each side; Altai Mountains.....
   .....*Deuterophlebia* sp.
3. With a pair of short, thin, transverse, heavily sclerotized bands near the midline of most of the abdominal segments; without granulations on the last two abdominal segments; Honshu and Kyushu, Japan.....
   .....*D. nipponica* Kitakami
   Without such abdominal bands; granulations present on the last two abdominal segments.....4
4. With a pair of long, thin, transverse, heavily sclerotized bands on the mesothorax; northern Colorado....
   .....*D. coloradensis*, new species
   Without such mesothoracic bands; mountainous areas of central Asia..
   .....*D. mirabilis* Edwards

The known geographical distribution of *Deuterophlebia* is an interesting one. The genus is widely distributed throughout the mountainous areas of central Asia as far south as the Himalayas. It occurs in northern Korea, and on the islands of Honshu and Kyushu in Japan. In North America it is known from Wyoming, Colorado, California, and Oregon, and it is likely that a search would show that it occurs throughout the mountainous western states and perhaps Canada. From the

TABLE 2

MORPHOLOGICAL COMPARISON OF MATURE LARVAE OF THE FOUR ESTABLISHED SPECIES OF *Deuterophlebia*

Species	Ratio of basal segment:ventral branch:dorsal branch of antennae	Average number of rings of hooks on prolegs	Average length, mm.
D. mirabilis Edwards	1:1:1.25	13 to 14	4.0 to 5.0
D. nipponica Kitakami	1:1:2–3	9 to 12	2.8 to 4.3
D. tyosenensis Kitakami	1:0.9:1.8	9 to 11	3.6
D. coloradensis, new species	1:1:2	9 to 11	3.9

standpoint of ecological requirements, the immature stages of *Deuterophlebia* in these areas appear to be confined to rapid, clear streams having rocky bottoms and summer temperatures below 19° C. Theoretically, therefore, it could occur in such places as the northern Appalachian Mountains and the mountainous portions of Europe. It is particularly striking that the genus has never been reported from the Alps and associated areas, especially since the bottom fauna of alpine streams has been studied more intensively than that of any other group of mountain streams. It appears logical to infer that the genus does not occur in Europe. Aside from the aquatic stages, however, the geographical distribution of *Deuterophlebia* is probably largely determined by certain habits of the imago. The facts that they are never abundant, do not feed, and are feeble fliers, for example, would all tend to decrease markedly their rate of geographical spread.

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